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Unveiling hidden diversity in *Odorrana* (Anura, Ranidae) with description of a new species from Yingjiang, China and the first national records of *Odorrana heatwolei* in Thailand and Vietnam

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Abstract

Species discovery within *Odorrana* has gradually increased over the years, establishing a remarkable diversity for the genus. During recent herpetological surveys, we collected specimens from Yingjiang County, Yunnan Province, China with additional samples from Thailand and Vietnam. Based on combined morphological and phylogenetic analyses, we describe a new species *Odorrana sudianensis* **sp. nov.** from Sudian Town, Yingjiang County, China and report new records of *O. heatwolei* for Thailand and Vietnam. Phylogenetic analyses, based on the 16S rRNA mitochondrial gene fragment, confirm the new species as a distinct evolutionary lineage with a genetic divergence (*p*-distance) of 4.6% from its closest sister species *O. dulongensis*. *Odorrana sudianensis* **sp. nov.** is morphologically distinguishable from all its known congeners by having a robust medium adult body size, a head length longer than wide, a mottled grass-green dorsum with dark brown blotches on the posterior region, absence of dorsolateral folds and circum-marginal grooves for all finger discs expanded with lateroventral grooves. Additionally, the new species record sequences from Thailand and Vietnam nested within the *O. heatwolei* subclade with a low *p*-distance (0.0–0.5%) from topotypic sequences of *O. heatwolei*. Examined specimen shows morphological congruence with topotypic *O. heatwolei* in key diagnostic traits. Our new species and new species records increase the number of recognised species of *Odorrana* to 46 in China, seven in Thailand and 23 in Vietnam. We also address existing taxonomic disputes within *Odorrana* and provide comments and recommendations on the taxonomy of several species within the genus.

Key Words

Odorrana, Indo-Burma biodiversity hotspot, new species, new species record, *Odorrana sudianensis* sp. nov., taxonomy

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Introduction

The Indo-Burma biodiversity hotspot is globally recognised for its extraordinary species diversity, characterised by its highly threatened and endemic biota (Mittermeier et al. 1999, 2004, 2011; Myers et al. 2000). The region's exceptional species richness is shaped by the complex topography greatly influenced by mountain ecosystems, diverse habitats ranging from tropical rainforests to karstic landscapes and a dynamic history that has fostered speciation (Das and van Dijk 2013; De Bruyn et al. 2014; Poyarkov et al. 2021). Amphibian diversity across these regions was historically underestimated. However, efforts to elucidate diversity within amphibian species complexes, widespread species and cryptic lineages with the application of integrated taxonomy have led to significant progress in the discoveries of new species (e.g. Li et al. (2012); Chen et al. (2017, 2018); Poyarkov et al. (2020); Chan et al. (2020); Wu et al. (2020, 2025); Trofimets et al. (2024)).

The genus *Odorrana* Fei, Ye & Huang, 1990 comprises frogs commonly known as Odorous frogs in the family Ranidae (Frost 2025). It is one of the most speciose amphibian genera and is widely distributed across Japan, southern China, north-eastern India and Southeast Asia through Myanmar, Vietnam, Laos, Thailand, Cambodia and south to Malaysia and Indonesia (Frost 2025). Following previous taxonomic revisions, the genus is considered monophyletic with *O. margaretae* (Liu, 1950) as the type species (Che et al. 2007; Stuart 2008; Pyron and Wiens 2011; Chen et al. 2013). At present, 67 species are recognised (Frost 2025) with a sizable proportion (45 species) documented in China (AmphibiaChina 2025), establishing it as a hotspot for Odorous frogs. Over the last decade, 14 new species have been described, including three recently described: *O. damingshanensis* Chen, Mo, Lin & Qin, 2024, *O. leishanensis* Li, Chen, Su, Liu, Tang & Wang, 2024 and *O. calciphila* Song, Qi, Wang, Liu & Wang, 2025. These recent findings are consistent with numerous studies indicating that diversity within this genus remains significantly underestimated (Pham et al. 2016; Liu et al. 2021; Li et al. 2024). Over the years, the genus *Odorrana* has presented taxonomic challenges as most species are morphologically conservative making it difficult to correctly distinguish them solely based on morphology (Wang et al. 2015). The adoption of integrative taxonomic approaches that combine molecular data and morphological characters has proven critical in resolving these challenges as well as uncovering cryptic diversity.

During our field surveys at Yingjiang County, Yunnan Province, China, we collected two *Odorrana* specimens that could not be assigned to any known species. Separately, three samples were previously collected during fieldwork expeditions in Nan and Phitsanulok Provinces, northern Thailand, on different occasions, with four additional samples (including one specimen) collected from Dien Bien Province, in the north-western border region of Vietnam. Subsequent molecular analyses identified these populations as a new species and new national species records, respectively. Herein, we describe the new species from Sudian Town, Yingjiang County, close to the China-Myanmar border and report the new species records for Thailand and Vietnam.

Materials and methods

Taxon sampling

Two *Odorrana* specimens were collected from Sudian, Yingjiang County, Yunnan Province, China. In addition, seven tissue samples were previously collected from Nan and Phitsanulok Provinces in northern Thailand and Dien Bien Province in Vietnam on different occasions (Fig. 1, Table 1). Geographical coordinates were taken by a GPS (Global Positioning System) in decimal degrees. The specimens were photographed and humanely euthanised using benzocaine. Tissue samples from muscle or liver were extracted and stored in 95% ethanol. Voucher specimens were fixed in 10% buffered formalin, after which they were subsequently preserved in 75% ethanol for permanent storage at the Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ, CAS), Field Museum of Natural History (FMNH), University of Kansas (KU) and the University of Phayao. Research protocols were approved by the Ethics Research Committee of the Kunming Institute of Zoology, Chinese Academy of Sciences (IACUC number: IACUC-OE-2021-07-001).

Morphological analysis

The sex and maturity of the specimens were determined by identifying secondary sexual characteristics, such as the presence of vocal sacs in males and visible eggs in gravid females. External morphological characteristics were examined with morphological measurements obtained using digital calipers taken to the nearest 0.1 mm. Morphological characters examined followed Fei et al. (2009) with slight modifications to meet the current research standards. Measurements were taken as follows: **SVL** (snout-vent length), from tip of snout to vent; **HL** (head length), from tip of snout to the jaw angle; **HW** (head width), the width of the head at its widest point; **SL** (snout length), from tip of snout to anterior corner of eye; **IND** (internasal distance), distance between nares; **IOD** (interorbital distance), the narrowest point between eyelids on top of head as the minimum distance between upper eyelids; **NED** (nasal to eye distance), distance from the anterior corner of eye

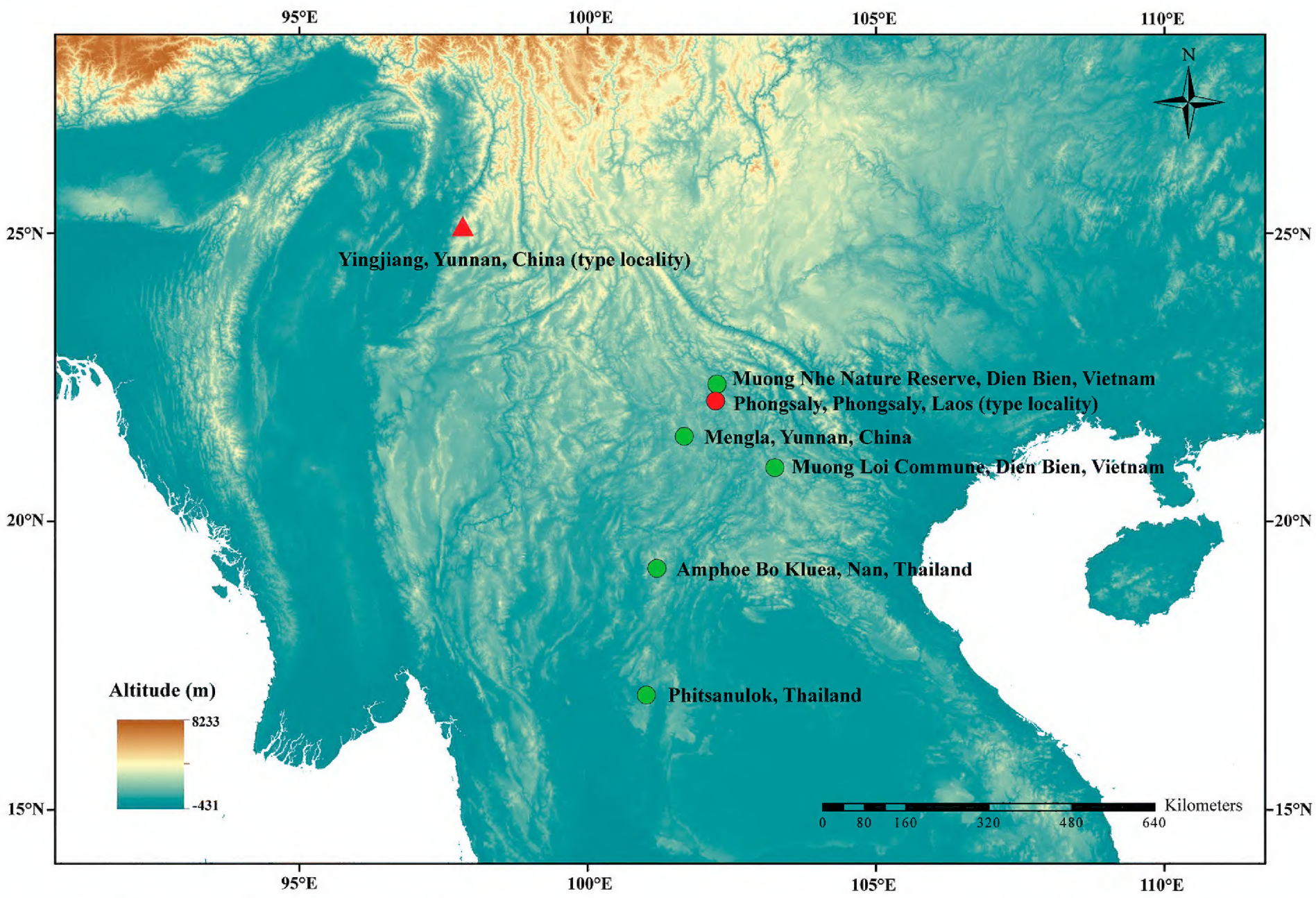

Figure 1. Map showing the type locality of *Odorrana sudianensis* sp. nov. (red triangle) and the type locality of *Odorrana heatwolei* in Laos (red circle); (green circles) indicate other collection locations of *Odorrana heatwolei* in China, Thailand and Vietnam.

to center of the nostril; **SND** (snout-nostril distance), distance from nostril centre to the snout tip; **UEW** (upper eyelid width), maximum width of the upper eyelid; **ED** (eye diameter), distance between corners of eye; **TD** (tympanum diameter), maximum horizontal diameter of the tympanum; **TYE** (tympanum-eye distance), distance from anterior border of tympanum to posterior orbital border; **FAHL** (forearm and the hand length), the total fore-limb extension measured as the distance from elbow to the tip of the third finger; **HND** (hand length), from the proximal edge of inner metacarpal tubercle to the tip of third finger; **LAD** (diameter of lower arm) maximum diameter of the lower arm measured at its widest point; **FAL** (forearm length), from the elbow to the wrist; **HLL** (hind-limb length), from the tip of the fourth toe to vent; **FEM** (femoral length), from the cloaca to the knee; **TIB** (tibia length), from knee to heel; **FTL** (foot length), from proximal end of inner metatarsal tubercle to the tip of fourth toe; **FIL** (first finger length); **FIIL** (second finger length); **FIIIL** (third finger length); **FIVL** (fourth finger length); **TIL** (first toe length); **TIIL** (second toe length); **TIIIL** (third toe length); **TIVL** (fourth toe length); **TVL** (fifth toe length) (Table 4). Morphological data for comparison with several congeners under the genus *Odorrana* used in this study were taken from available published literature (see Table 5).

DNA extraction, PCR amplification and Sequencing

Total genomic DNA was extracted from muscle or liver tissues using the standard phenol-chloroform extraction protocol (Sambrook et al. 1989). To identify the species, a fragment of mitochondrial 16S ribosomal RNA gene (16S rRNA) was amplified and sequenced using the primer pairs 16SAR (5'–CGCCTGTTTAYCAAAAACAT–3') and 16SBR (5'–CCGGTYTGAACTCAGATCAYGT–3') (Kocher et al. 1989) for all our new samples. Amplifications (Polymerase Chain Reaction, PCR) were performed in a 25 µl reaction volume containing 17.75 µl of double distilled water (ddH_2O), 2.5 µl of PCR buffer, 1.0 µl of dNTPs mix, 1.0 µl of forward primer (16SAR), 1.0 µl of reverse primer (16SBR), 0.25 µl of Taq DNA polymerase and 1.5 µl of template DNA. The following cycling conditions were used: an initial denaturing step at 94 °C for 5 min, 35 cycles of denaturing at 94 °C for 45s, annealing at 46 °C for 30s, extension at 72 °C for 1 min and a final extension step of 72 °C for 10 min. Amplified PCR products were sequenced using an ABI 3730xl DNA automated sequencer (Applied Biosystems, UK). All newly-generated sequences were assembled from forward to reverse reads and trimmed manually using SeqMan in DNASTAR LASERGENE 7.1 (Burland 2000). The sequences have been deposited in the DNA Data Bank of Japan (Table 1).

Table 1. Voucher information, localities and accession numbers for all sequences used in molecular analyses of this study. A (/) indicates information absent "*" indicates sequences derived from the holotype or paratype, while "#" indicates sequences derived from the type locality.

ID	Species	Locality	Voucher number	Accession No. (16S)	Reference
Ingroups					
1	*Odorrana sudianensis* sp. nov.	Sudian town, Yingjiang county, Yunnan, China	KIZ 058904	LC902022	This study
2	*Odorrana sudianensis* sp. nov.	Sudian town, Yingjiang county, Yunnan, China	KIZ 058839	LC902021	This study
3	*Odorrana heatwolei*	Ban Sapan, Amphoe Bo Kluea, Nan, Thailand	FMNH 270729	LC902023	This study
4	*Odorrana heatwolei*	Ban Sapan, Amphoe Bo Kluea, Nan, Thailand	FMNH 270730	LC902024	This study
5	*Odorrana heatwolei*	Muong Nhe Nature Reserve, Dien Bien, Vietnam	KU 331577	LC902027	This study
6	*Odorrana heatwolei*	Muong Nhe Nature Reserve, Dien Bien, Vietnam	KU 331572	LC902026	This study
7	*Odorrana heatwolei*	Muong Nhe Nature Reserve, Dien Bien, Vietnam	KU 331568	LC902025	This study
8	*Odorrana heatwolei*	Phu Hin Rong Kla National Park, Phitsanulok, Thailand	P-08117	LC902018	This study
9	*Odorrana heatwolei*	Muong Loi Commune, Dien Bien Prov, Vietnam	ITBCZ 3660	LC902019	This study
10	*Odorrana yunnanensis*	Sudian town, Yingjiang county, Yunnan, China	KIZ 058903	LC902020	This study
11	*Odorrana leishanensis*	Leigongshan Nature Reserve, Leishan, Guizhou, China	MT LS20230806010*	OR879754	Li et al. (2024)
12	*Odorrana leishanensis*	Leigongshan Nature Reserve, Leishan, Guizhou, China	MT LS20230729013*	OR879757	Li et al. (2024)
13	*Odorrana fengkaiensis*	Heishiding Nature Reserve, Fengkai, Guangdong, China	SYS a002262*	KT315375	Wang et al. (2015)
14	*Odorrana fengkaiensis*	Heishiding Nature Reserve, Fengkai, Guangdong, China	SYS a002263*	KT315376	Wang et al. (2015)
15	*Odorrana bacboensis*	Vietnam	IEBR 3942	KX893909	Unpublished
16	*Odorrana bacboensis*	Vietnam	IEBR A.2015.83	KX893887	Unpublished
17	*Odorrana bacboensis*	Vietnam	VFUKH 073	KX893888	Unpublished
18	*Odorrana damingshanensis*	Wuming, Guangxi, China	NNU00690*	ON791420	Chen et al. (2024)
19	*Odorrana hainanensis*	Wuzhishan city, Hainan, China	HNNU0606105#	KF185032	Wang et al. (2015)
20	*Odorrana bacboensis*	Bainan village, Napo, Guangxi, China	SYS a001046	KT315385	Wang et al. (2015)
21	*Odorrana bacboensis*	Khe Moi, Nghe An,Vietnam	FMNH255611	DQ650569	Chen et al. (2005)
22	*Odorrana bacboensis*	Hekou, Yunnan, China	HNNU HK001	KF185044	Chen et al. (2013)
23	*Odorrana bacboensis*	Vietnam	ZFMK-80106	KX893908	Unpublished
24	*Odorrana bacboensis*	Vietnam	ZFMK-80109	KX893910	Unpublished
25	*Odorrana schmackeri*	Yichang City, Hubei, China	HNNU0908II349#	KF185047	Chen et al. (2013)
26	*Odorrana kweichowensis*	Lengshuihe Nature Reserve, Jinsha, Guizhou, China	CIBjs20150803008*	MH193552	Li et al. (2018)
27	*Odorrana kweichowensis*	Lengshuihe Nature Reserve, Jinsha, Guizhou, China	CIBjs20171014001* (tadpole)	MH193551	Li et al. (2018)
28	*Odorrana sangzhiensis*	Sangzhi, Hunan, China	CSUFT 4308220046*	MW464864	Zhang et al. (2021)
29	*Odorrana sangzhiensis*	Sangzhi, Hunan, China	CSUFT 4308220051*	MW464865	Zhang et al. (2021)
30	*Odorrana ichangensis*	Zhijin, Guizhou, China	MT ZJ20210814004	OR879767	Li et al. (2024)
31	*Odorrana ichangensis*	Yichang City, Hubei, China	SYS a005475	OR879765	Li et al. (2024)
32	*Odorrana hejiangensis*	Chishui, Guizhou, China	MT CS20200605008	OR879764	Li et al. (2024)
33	*Odorrana hejiangensis*	Hejiang, Sichuan, China	HNNU1007-202#	KF185052	Chen et al. (2013)
34	*Odorrana nanjiangensis*	Nanjiang, Sichuan China	HNNU1007-291#	KF185042	Chen et al. (2013)
35	*Odorrana tianmuii*	Lin'an, Zhejiang, China	HNNU707071*	KF185040	Chen et al. (2013)
36	*Odorrana tianmuii*	Mt. Tianmu, Lin'an, Zhejiang, China	SYS a002680	OR879761	Li et al. (2024)
37	*Odorrana huanggangensis*	Leigongshan Nature Reserve, Leishan, Guizhou, China	CIBLS20140818005	MH193564	Li et al. (2018)
38	*Odorrana versabilis*	Leigongshan Nature Reserve, Leishan, Guizhou, China	HNNU003#	KF185055	Chen et al. (2013)
39	*Odorrana nasuta*	Wuzhishan, Hainan, China	HNNU051119#	KF185053	Chen et al. (2013)
40	*Odorrana exiliversabilis*	Wuyishan, Fujian, China	HNNU0607032#	KF185056	Chen et al. (2013)
41	*Odorrana yentuensis*	Guangxi, China	NHMG1401035	MH665675	Mo et al. (2015)
42	*Odorrana yentuensis*	Vietnam	IEBR A.2015.38	KX893891	Unpublished
43	*Odorrana nasica*	HaTinh, Vietnam	AMNH A161169	DQ283345	Frost et al. (2006)
44	*Odorrana tormota*	Huangshan, Anhui, China	AM04005#	DQ835616	Su et al. (2007)
45	*Odorrana tormota*	Huangshan, Anhui, China	SCUM052069	NC009423	Su et al. (2007)
46	*Odorrana narina*	Okinawa Island, Japan	/	AB511287	Kurabayashi et al. (2010)
47	*Odorrana amamiensis*	Tokunoshima, Ryukyu, Japan	KUHE:24635	AB200947	Matsui et al. (2005)
48	*Odorrana supranarina*	Iriomotejima, Ryukyu	KUHE:12898	AB200950	Matsui et al. (2005)
49	*Odorrana swinhoana*	Nantou, Taiwan, China	HNNUTW9	KF185046	Chen et al. (2013)
50	*Odorrana hosii*	Kuala Lumpur, Malaysia	IABHU 21004	AB511284	Kurabayashi et al. (2010)
51	*Odorrana graminea*	Wuzhishan, Hainan, China	HNNU0606123#	KF185038	Chen et al. (2013)
52	*Odorrana chloronota*	Ha Giang, Vietnam	AMNH A163935	DQ283394	Frost et al. (2006)
53	*Odorrana livida*	Prachuap Kirikhan, Thailand	FMNH 263415	DQ650613	Stuart et al. (2006)
54	*Odorrana livida*	Myanmar, Thagata Juwa Village	BMNH 1889.3.25.48 Neotype	DQ650615	Stuart et al. (2006)
55	*Odorrana leporipes*	Shaoguan, Guangdong, China	HNNU1008-099#	KF185036	Chen et al. (2013)
56	*Odorrana aureola*	Thailand, Loei Province, Phu Ruea District	FMNH 265925*	DQ650568	Stuart et al. (2006)
57	*Odorrana aureola*	Thailand, Loei Province, Phu Ruea District	FMNH 265923*	DQ650567	Stuart et al. (2006)

ID	Species	Locality	Voucher number	Accession No. (16S)	Reference
58	*Odorrana morafkai*	Tram Lap, Vietnam	ROM 7446	AF206484	Chen et al. (2005)
59	*Odorrana banaorum*	Tram Lap, An Khe District, Gia Lai Province Vietnam	ROM 39913*	DQ650586	Stuart et al. (2006)
60	*Odorrana banaorum*	Tram Lap, An Khe District, Gia Lai Province Vietnam	ROM 39901*	DQ650588	Stuart et al. (2006)
61	*Odorrana junlianensis*	Junlian, Sichuan, China	HNNU002JL#	KF185058	Chen et al. (2013)
62	*Odorrana grahami*	Kunming, Yunnan, China	HNNU1008-016#	KF185051	Chen et al. (2013)
63	*Odorrana hmongorum*	Lao Cai, Vietnam	ROM 38605	EU861556	Bain et al. (2009)
64	*Odorrana andersonii*	Longchuan County, Yunnan, China	HNNU001YN#	KF185057	Chen et al. (2013)
65	*Odorrana jingdongensis*	Jingdong, Yunnan, China	20070711017#	KF185050	Chen et al. (2013)
66	*Odorrana margaretae*	Mt. Emei, Sichuan, China	HNNU20050032	KF185035	Chen et al. (2013)
67	*Odorrana margaretae*	Mt. Qingchengshan, Dujiangyan City, Sichuan, China	SYS a003214	KT315391	Wang et al. (2015)
68	*Odorrana kuangwuensis*	Nanjiang, Sichuan, China	HNNU0908I185#	KF185034	Chen et al. (2013)
69	*Odorrana dulongensis*	Dulongjiang, Gongshan county, Yunnan, China	KIZ035027*	MW128102	Liu et al. (2021)
70	*Odorrana dulongensis*	Dulongjiang, Gongshan county, Yunnan, China	KIZ035028*	MW128103	Liu et al. (2021)
71	*Odorrana dulongensis*	Dulongjiang, Gongshan county, Yunnan, China	KIZ035029*	MW128104	Liu et al. (2021)
72	*Odorrana dulongensis*	Dulongjiang, Gongshan county, Yunnan, China	KIZ035030*	MW128105	Liu et al. (2021)
73	*Odorrana wuchuanensis*	Wuchuan, Guizhou Prov., China	HNNU019L#	KF185043	Chen et al. (2013)
74	*Odorrana mutschmanni*	Cao Bang, Vietnam	IEBR 3725*	KU356766	Pham et al. (2016)
75	*Odorrana mutschmanni*	Cao Bang Province, Vietnam	IEBR 3723*	KU356765	Pham et al. (2016)
76	*Odorrana yizhangensis*	Yizhang, Hunan	HNNU1008I075#	KF185048	Chen et al. (2013)
77	*Odorrana lungshengensis*	Longsheng, Guangxi	HNNU70028#	KF185054	Chen et al. (2013)
78	*Odorrana anlungensis*	Anlong, Guizhou, China	HNNU1008I109#	KF185049	Chen et al. (2013)
79	*Odorrana chapaensis*	Mount Fansipan, Lai Chau, Vietnam	AMNH A161439	DQ283372	Frost et al. (2006)
80	*Odorrana geminata*	Cao Bo, Ha Giang, Vietnam	AMNH 163782*	EU861546	Bain et al. (2009)
81	*Odorrana absita*	Xe Sap, Xe Kong, Laos	FMNH 258109*	EU861542	Bain et al. (2009)
82	*Odorrana liboensis*	Maolan National Nature Reserve, Libo, Guizhou, China	GZNU20180608007*	MW481350	Luo et al. (2021)
83	*Odorrana lipuensis*	Lipu, Guangxi, China	NHMG1303018*	MH665676	Mo et al. (2015)
84	*Odorrana concelata*	Longlinchang Village, Qingyuan, Guangdong,China	GEP a050*	OP137161	Lin et al. (2022)
85	*Odorrana heatwolei*	Phongsaly, Phongsaly, Laos	FMNH 258134*	OR237216	Liu et al. (2023)
86	*Odorrana heatwolei*	Mengla, Yunnan, China	KIZ20194301	OR237218	Liu et al. (2023)
87	*Odorrana heatwolei*	Mengla, Yunnan, China	KIZ20194302	OR237219	Liu et al. (2023)
88	*Odorrana heatwolei*	Mengla, Yunnan, China	KIZ20194255	OR237220	Liu et al. (2023)
89	*Odorrana tiannanensis*	Gejiu, Yunnan, China	KIZ20193242	OR237225	Liu et al. (2023)
90	*Odorrana tiannanensis*	Hekou, Yunnan, China	KIZ20193272#	OL831009	Liu et al. (2022)
91	*Odorrana tiannanensis*	Hekou, Yunnan, China	KIZ20193273#	OL831008	Liu et al. (2022)
92	*Odorrana tiannanensis*	Malipo, Yunnan, China	KIZ20215122	OR237228	Liu et al. (2023)
93	*Odorrana macrotympana*	Xueli Village, Taiping Town, Yingjiang, Yunnan, China	KIZ 2009051020#	OL831010	Liu et al. (2022)
94	*Odorrana macrotympana*	Htamanthi, Sagaing, Myanmar	SEABRI 2019120040	OL831011	Liu et al. (2022)
Outgroups					
95	*Nidirana daunchina*	Emeishan, Sichuan, China	HNNU20060103#	KF185065	Chen et al. (2013)
96	*Amolops loloensis*	Shimian, Sichuan, China	SM-ZDTW-01	NC_029250	Xue et al. (2016)
97	*Pelophylax nigromaculata*	Hongya, Sichuan, China	SCUM045199CJ	KX269216	Yuan et al. (2016)

Phylogenetic analyses

The assembled 16S rRNA sequences were initially aligned using the ClustalW algorithm (Thompson et al. 1997) and realigned using MUSCLE 3.8 (Edgar 2004) with default settings in MEGA v.6.0 (Tamura et al. 2013). Sequences were visually checked by eye for accuracy and trimmed to minimise missing characters. In addition to the newly-generated sequences, 87 homologous sequences for the genus *Odorrana* and three outgroup taxa *Nidirana daunchina* (Chang, 1933), *Pelophylax nigromaculatus* (Hallowell, 1861) and *Amolops loloensis* (Liu, 1950), were downloaded from GenBank. Whenever possible, we ensured that the sequences included were either holotypes, paratypes or topotypes to accurately define the true clades for the genus and correctly delimit species boundaries. In total, our sequence matrix included 53 representative species for the genus *Odorrana*; however, not all species had sequence information available in GenBank as some species including *O. arunachalensis* Saikia, Sinha & Kharkongor, 2017; *O. bolavensis* (Stuart & Bain, 2005); *O. cangyuanensis* (Yang, 2008); *O. gigatympana* (Orlov, Ananjeva & Ho, 2006); *O. indeprensa* (Bain & Stuart, 2006); *O. orba* (Stuart & Bain, 2005); *O. sinica* (Ahl, 1927) and *O. monjerai* (Matsui & Jaafar, 2006)), described solely based on morphology, lacked sequence data at present.

We inferred phylogenetic relationships by reconstructing phylogenetic trees using Maximum Likelihood (ML) and Bayesian Inference (BI) approaches. Both the BI and ML analyses were performed on the CIPRES web server (Miller et al. 2010). BI analyses were performed using MrBayes v.3.2.4 (Ronquist et al. 2012). The TIM2+I+G model was selected as the best-fit substitution model, based on the Bayesian Information Criterion (BIC; Posada (2008)) by jModelTest2 (Darriba et al. 2012). Two independent runs were conducted and a Monte Carlo Markov chain length was run for ten million generations and sampled every 1000 generations with a burn-in of 25%

after the standard deviation of split frequencies for the two runs was less than 0.01. The remaining trees were used to create a 50% majority rule consensus tree and to estimate Bayesian posterior probabilities (BPP). ML analyses were performed using RAxML-HPC BlackBox 8.2.10 (Stamatakis 2014) with 1,000 bootstrap replicates. The resulting bootstrap support values (BS) were used to assess nodal support. The mean genetic distances amongst individuals on the 16S rRNA dataset were calculated using the uncorrected sequence divergence (*p*-distance model) implemented in MEGA v.6.0 with pairwise deletion of missing data and gaps (Tamura et al. 2013).

Results

Phylogenetic analyses

Using combined morphological examination and molecular analyses, our results confirmed that *Odorrana* specimens collected from Yingjiang County, Yunnan Province, China represent a distinct undescribed lineage. Additionally, the analyses accurately identified samples from Thailand and Vietnam as new country records.

Our aligned sequence matrix for the 16S rRNA gene for all 97 individual sequences and outgroups comprised a total of 665 base pairs with 359 conserved sites, 298 variable sites and 234 parsimony informative sites. Both BI and ML trees recovered largely congruent tree topologies with relatively high nodal support values, which slightly differed between methods (BPP = 1; BS = 94; Fig. 2). The samples (voucher numbers KIZ 058839 and KIZ 058904) from Sudian, Yingjiang County clustered within a monophyletic genus *Odorrana* and represented a deeply-divergent undescribed genetic lineage. The Sudian population (described below) was recovered as a sister taxon to *O. dulongensis* Liu, Che & Yuan, 2021 with a relatively strong node support value (BPP = 1; BS = 95) within a larger partially supported clade (Clade E, BPP < 0.95; BS = 76) consisting of *O. margaretae*, *O. kuangwuensis* (Liu & Hu, 1966), *O. jingdongensis* Fei, Ye & Li, 2001, *O. yunnanensis* (Anderson, 1879),

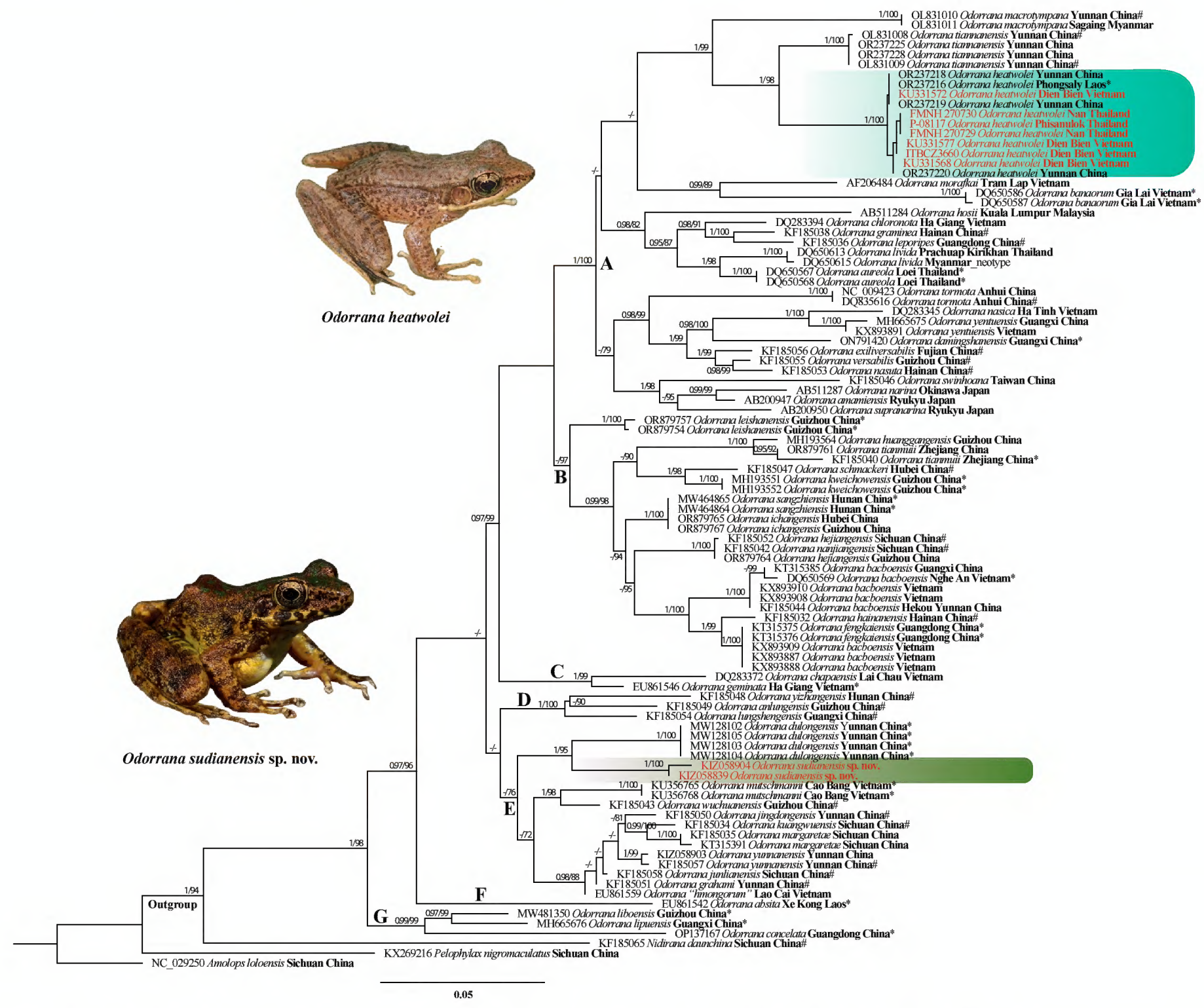
Odorrana heatwolei
Odorrana sudianensis sp. nov.
OL831010 Odorrana macrotympana Yunnan China#
OL831011 Odorrana macrotympana Sagaing Myanmar
OL831008 Odorrana tiannanensis Yunnan China#
OR237225 Odorrana tiannanensis Yunnan China
OR237228 Odorrana tiannanensis Yunnan China
OL831009 Odorrana tiannanensis Yunnan China#
OR237218 Odorrana heatwolei Yunnan China
OR237216 Odorrana heatwolei Phongsaly Laos*
KU331572 Odorrana heatwolei Dien Bien Vietnam
OR237219 Odorrana heatwolei Yunnan China
FMNH 270730 Odorrana heatwolei Nan Thailand
P-08117 Odorrana heatwolei Phisamulok Thailand
FMNH 270729 Odorrana heatwolei Nan Thailand
KU331577 Odorrana heatwolei Dien Bien Vietnam
ITBCZ3660 Odorrana heatwolei Dien Bien Vietnam
KU331568 Odorrana heatwolei Dien Bien Vietnam
OR237220 Odorrana heatwolei Yunnan China
AF206484 Odorrana morafkai Tram Lap Vietnam
DQ650586 Odorrana banaorum Gia Lai Vietnam*
DQ650587 Odorrana banaorum Gia Lai Vietnam*
AB511284 Odorrana hosii Kuala Lumpur Malaysia
DQ283394 Odorrana chloronota Ha Giang Vietnam
KF185038 Odorrana graminea Hainan China#
KF185036 Odorrana leporipes Guangdong China#
DQ650613 Odorrana livida Prachuap Kirikhan Thailand
DQ650615 Odorrana livida Myanmar_neotype
DQ650567 Odorrana aureola Loei Thailand*
DQ650568 Odorrana aureola Loei Thailand*
NC_009423 Odorrana tormota Anhui China
DQ835616 Odorrana tormota Anhui China#
DQ283345 Odorrana nasica Ha Tinh Vietnam
MH665675 Odorrana yentuensis Guangxi China
KX893891 Odorrana yentuensis Vietnam
ON791420 Odorrana damingshanensis Guangxi China*
KF185056 Odorrana exiliversabilis Fujian China#
KF185055 Odorrana versabilis Guizhou China#
KF185053 Odorrana nasuta Hainan China#
KF185046 Odorrana swinhoana Taiwan China
AB511287 Odorrana narina Okinawa Japan
AB200947 Odorrana amamiensis Ryukyu Japan
AB200950 Odorrana supranarina Ryukyu Japan
OR879757 Odorrana leishanensis Guizhou China*
OR879754 Odorrana leishanensis Guizhou China*
MH193564 Odorrana huanggangensis Guizhou China
OR879761 Odorrana tianmuii Zhejiang China
KF185040 Odorrana tianmuii Zhejiang China*
KF185047 Odorrana schmackeri Hubei China#
MH193551 Odorrana kweichowensis Guizhou China*
MH193552 Odorrana kweichowensis Guizhou China*
MW464865 Odorrana sangzhiensis Hunan China*
MW464864 Odorrana sangzhiensis Hunan China*
OR879765 Odorrana ichangensis Hubei China
OR879767 Odorrana ichangensis Guizhou China
KF185052 Odorrana hejiangensis Sichuan China#
KF185042 Odorrana nanjiangensis Sichuan China#
OR879764 Odorrana hejiangensis Guizhou China
KT315385 Odorrana bacboensis Guangxi China
DQ650569 Odorrana bacboensis Nghe An Vietnam*
KX893910 Odorrana bacboensis Vietnam
KX893908 Odorrana bacboensis Vietnam
KF185044 Odorrana bacboensis Hekou Yunnan China
KF185032 Odorrana hainanensis Hainan China#
KT315375 Odorrana fengkaiensis Guangdong China*
KT315376 Odorrana fengkaiensis Guangdong China*
KX893909 Odorrana bacboensis Vietnam
KX893887 Odorrana bacboensis Vietnam
KX893888 Odorrana bacboensis Vietnam
DQ283372 Odorrana chapaensis Lai Chau Vietnam
EU861546 Odorrana geminata Ha Giang Vietnam*
KF185048 Odorrana yizhangensis Hunan China#
KF185049 Odorrana anlungensis Guizhou China#
KF185054 Odorrana lungshengensis Guangxi China#
MW128102 Odorrana dulongensis Yunnan China*
MW128105 Odorrana dulongensis Yunnan China*
MW128103 Odorrana dulongensis Yunnan China*
MW128104 Odorrana dulongensis Yunnan China*
KIZ058904 Odorrana sudianensis sp. nov.
KIZ058839 Odorrana sudianensis sp. nov.
KU356765 Odorrana mutschmanni Cao Bang Vietnam*
KU356768 Odorrana mutschmanni Cao Bang Vietnam*
KF185043 Odorrana wuchuanensis Guizhou China#
KF185050 Odorrana jingdongensis Yunnan China#
KF185034 Odorrana kuangwuensis Sichuan China#
KF185035 Odorrana margaretae Sichuan China
KT315391 Odorrana margaretae Sichuan China
KIZ058903 Odorrana yunnanensis Yunnan China
KF185057 Odorrana yunnanensis Yunnan China#
KF185058 Odorrana junlianensis Sichuan China#
KF185051 Odorrana grahami Yunnan China#
EU861559 Odorrana "hmongorum" Lao Cai Vietnam
EU861542 Odorrana absita Xe Kong Laos*
MW481350 Odorrana liboensis Guizhou China*
MH665676 Odorrana lipuensis Guangxi China*
OP137167 Odorrana concelata Guangdong China*
KF185065 Nidirana daunchina Sichuan China#
KX269216 Pelophylax nigromaculatus Sichuan China
NC_029250 Amolops loloensis Sichuan China
Outgroup
A
B
C
D
E
F
G
0.05

Figure 2. A Maximum Likelihood (ML) Phylogram of *Odorrana* inferred from 16S rRNA gene fragment (Node values with Bayesian posterior probabilities (BPP) < 0.95/Bootstrap support (BS) < 70 are not shown. A "–" denotes Bayesian posterior probabilities (BPP) < 0.95 and bootstrap support (BS) < 70, (*) denotes Holotype or Paratype and (#) denotes a Topotype. New samples for the present study are indicated in red font. Node values for outgroup taxa are not shown.

O. 'hmongorum' Bain, Lathrop, Murphy, Orlov & Ho, 2003, *O. grahami* (Boulenger, 1917), *O. junlianensis* Huang, Fei & Ye, 2001, *O. mutschmanni* Pham, Nguyen, Le, Bonkowski & Ziegler, 2016 and *O. wuchuanensis* (Xu, 1983). *Odorrana dulongensis* was described from Dulongjiang Village, Gongshan County, Nujiang Prefecture, Yunnan Province, China. The uncorrected sequence divergence (*p*-distance) between *O. dulongensis* and the Sudian population, based on the 16S rRNA gene, was 4.6% (Table 2), exceeding the threshold typically required for amphibian species delimitation (Vences et al. 2005; Fouquet et al. 2007).

Table 2. Mean uncorrected *p*-distances (%), based on 16S sequences between *Odorrana sudianensis* sp. nov. and *Odorrana dulongensis* species (lower matrix) and standard error estimates (upper matrix). The mean uncorrected *p*-distances are shown in bold.

Species	1	2	3	4	5	6
MW128102 *Odorrana dulongensis*		0.0	0.0	0.0	0.9	0.9
MW128103 *Odorrana dulongensis*	0.0		0.0	0.0	0.9	0.9
MW128104 *Odorrana dulongensis*	0.0	0.0		0.0	0.9	0.9
MW128105 *Odorrana dulongensis*	0.0	0.0	0.0		0.9	0.9
KIZ 058904 *Odorrana sudianensis* sp. nov.	**4.6**	**4.6**	**4.6**	**4.6**		0.4
KIZ 058839 *Odorrana sudianensis* sp. nov.	**4.6**	**4.6**	**4.6**	**4.6**	0.9	

In addition, seven *Odorrana* samples collected from Phitsanulok and Nan Provinces, northern Thailand and those collected from Dien Bien Province, Vietnam clustered with type sequences of *Odorrana heatwolei* (Stuart & Bain, 2005) with a strong nodal support (BPP = 1; BS = 100) (see clade A; Fig. 2). This molecular evidence verified the presence of *O. heatwolei* in Thailand and Vietnam, thus confirming the first national records of this species in these two countries. Molecular analyses revealed that these new sequences are nested within a distinct *O. heatwolei* subclade, with a pairwise uncorrected sequence divergence of less than 1.0% (0.0–0.5%) from the holotype sequences of *O. heatwolei* compared to 2.8–5.7% from the topotypic sequences of *O. tiannanensis* (Yang & Li, 1980), thus confirming the hypothesis of Liu et al. (2023) that *O. heatwolei* is the sister taxon of *O. tiannanensis* (Table 3). Notably, the subclade consisting of *O. jingdongensis*, *O. junlianensis*, *O. yunnanensis*, *O. kuangwuensis*, *O. margaritae* and *O. grahami* is weakly supported (BPP < 0.98; BS = 88) (see clade E).

Table 3. Mean uncorrected *p*-distances (%), based on 16S sequences between *Odorrana heatwolei* and *Odorrana tiannanensis* species (lower matrix) and standard error estimates (upper matrix). The mean uncorrected *p*-distances are shown on the diagonal in bold.

Species	1	2	3	4	5
Odorrana heatwolei Vietnam		0.14	0.18	0.11	0.73
Odorrana heatwolei Laos_Holotype	0.21		0.26	0.07	0.83
Odorrana heatwolei Thailand	0.25	0.43		0.22	0.70
Odorrana heatwolei China	0.17	0.09	0.36		0.83
Odorrana tiannanensis China	**4.86**	**5.57**	**3.89**	**5.57**	

Moreover, with the help of genetic data for 16S rRNA available in GenBank, we verify the phylogenetic placements and provide comments on the taxonomy of *O. bacboensis* (Bain, Lathrop, Murphy, Orlov & Ho, 2003), *O. fengkaiensis* Wang, Lau, Yang, Chen, Liu, Pang & Liu, 2015, *O. heatwolei*, *O. tiannanensis*, *O. nanjiangensis* Fei, Ye, Xie & Jiang, 2007, *O. hejiangensis* (Deng & Yu, 1992), *O. jingdongensis*, *O. 'hmongorum'*, *O. junlianensis*, *O. grahami* and *O. yunnanensis*.

We herein provide a detailed description of two specimens from Yingjiang, Yunnan Province, China, as a new species and provide additional morphological information on *O. heatwolei*.

Taxonomic accounts

Odorrana sudianensis Kilunda, Yu, Wu & Che, sp. nov.

https://zoobank.org/29048ACB-E02A-4061-B3A7-36FFA3052CA2

Figs 3, 4, 5A, B, Table 4

Type material. ***Holotype.*** KIZ 058904, adult female collected from Sudian Town, Yingjiang County, Yunnan Province, China (25°7.6446'N, 97°49.8402'E, 1563 m a.s.l.) on 2 December 2024 by Shen-Ping Yang, Shen-Quan Liu, and Jia-Sheng Liu.

Paratypes. KIZ 058839, an adult female, same collection information as the holotype, except for 25°7.4598'N, 97°49.8534'E, 1563 m a.s.l. on 4 September 2024.

Etymology. The specific epithet "sudianensis" is a latinised name referring to the type locality Sudian Town, where the new species was collected. We propose "Sudian odorous frog" and "苏典臭蛙" (Pinyin: Sū Diǎn Chòu Wā) as the English and Chinese common names, respectively.

Diagnosis. *Odorrana sudianensis* sp.nov. is assigned to the genus *Odorrana* and differs from its congeners based on the combination of the following morphological characters: (1) Robust medium adult body size (SVL 78.9–85.3 mm, based on two females); (2) head length longer than head width (HL/HW 1.08); (3) iris with intricate golden reticulations forming a circumpupillary ring around the periphery; (4) anterior part of dorsum mottled grass green with mottled dark brown blotches covering the posterior region; (5) dorsolateral folds absent; (6) distinct dark brown crossbands on the dorsal surface of limbs; (7) supratympanic fold obvious, weak and short; (8) dorsal and lateral skin slightly granular; (9) tongue cordiform, deeply notched posteriorly; (10) finger discs significantly expanded; (11) circummarginal grooves for all finger discs expanded with lateroventral grooves; (12) inner metacarpal tubercle, large and elongated, two outer metacarpal tubercles, with outer one larger than medial one; (13) supernumerary tubercles below the base of fingers present and rounded; (14) web on toes entirely covered; (15) inner metatarsal tubercle oval and present, outer metatarsal tubercle absent; supernumerary tubercles below the base of toes absent, subarticular tubercles of toes oval and prominent.

Figure 3. Morphology and colour patterns of *Odorrana sudianensis* sp. nov. in life (holotype KIZ058904, female). **A.** Lateral view; **B.** Ventral view; **C.** Ventral view of hand; **D.** Dorsal view; **E.** Dorsolateral view of head; **F.** Dorsal view of tarsus; photos by Shen-Pin Yang.

Description of holotype. Adult female KIZ 058904 (Figs 3, 4, Table 4), habitus robust, medium body size (SVL 85.3 mm); head length slightly longer than head width (HL/HW 1.08); snout length longer than the eye diameter (SL/ED 1.42); nostril oval, nostrils nearer to the tip of snout than to the eye (SND/NED 0.76); internarial distance greater than interorbital distance (IOD/IND 0.73); loreal region concave, oblique; interorbital area slightly flat in dorsal view (UEW/IOD 1.21); canthus rostralis distinctly visible, rounded; supratympanic fold obvious, weak and short, from the posterior edge of the eye to the corners of the mouth; tympanum clearly distinct with long curved irregular tubercles around it, smaller and shorter than eye diameter (half the eye diameter) (TD/ED 0.51); maxillary teeth developed; vomerine teeth developed, on two short obliques between choanae, obvious distance from each other; choanae oval; vocal sac absent; tongue cordiform, deeply notched posteriorly.

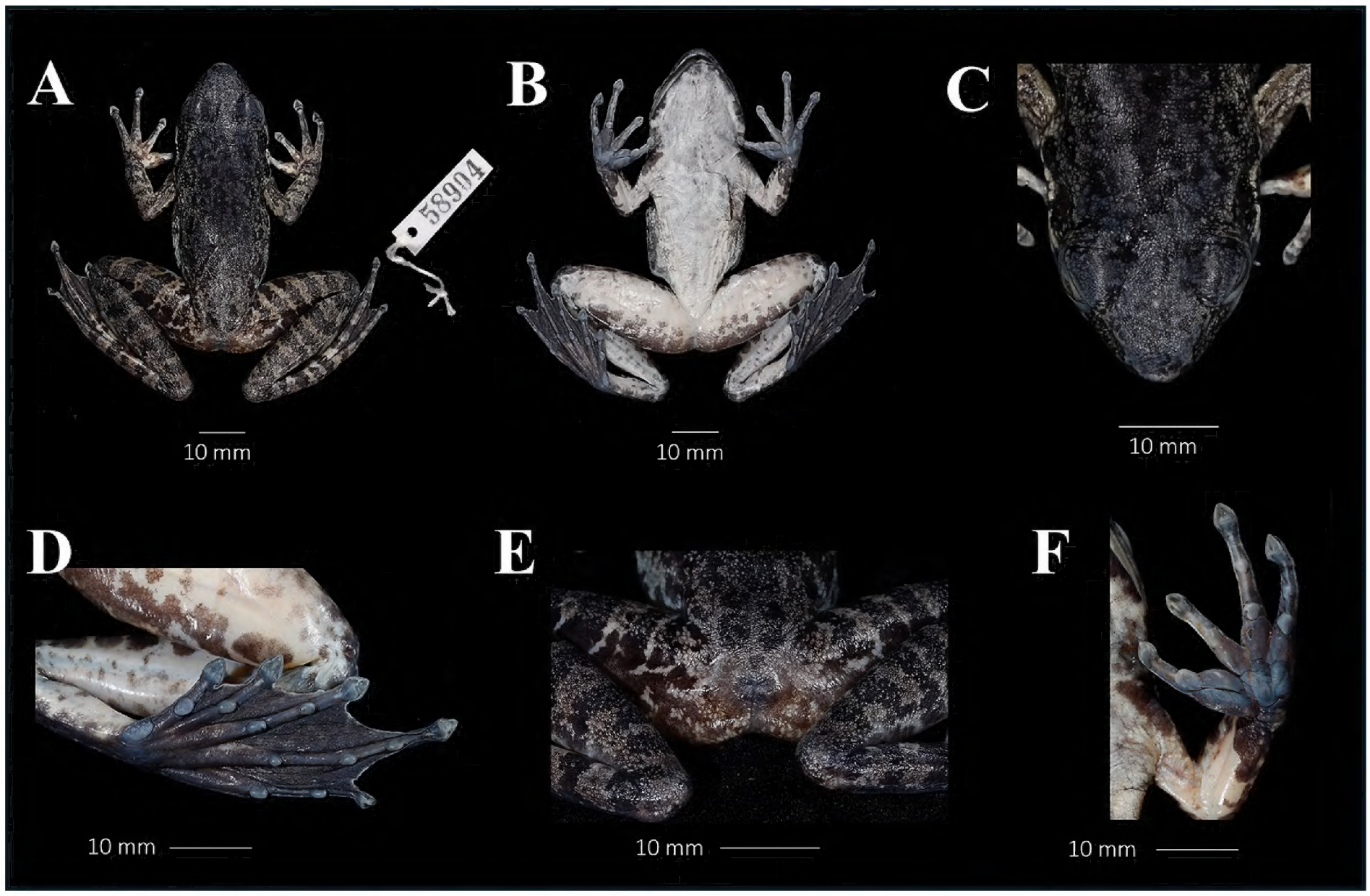

Figure 4. Holotype KIZ058904 of *Odorrana sudianensis* sp. nov. in preservative. **A.** Dorsal view; **B.** Ventral view; **C.** Dorsal view of head; **D.** Ventral view of foot; **E.** Dorsal view of cloacal region; **F.** Ventral view of hand; photos by Shen-Pin Yang.

Fore-limbs robust and shorter; nuptial pads absent; web on fingers absent; inner metacarpal tubercle, large and elongated; outer metacarpal tubercle two, oval, outer one larger than medial one; supernumerary tubercles below the base of fingers present and rounded; subarticular tubercles round and prominent; the tip of fingers expanded into discs, with disc largest in third finger; circum-marginal grooves for all finger discs expanded with lateroventral grooves; relative length of fingers (order III > I > IV > II).

Hind-limbs longer and muscular; tibia length longer than femur length FEM/TIB 0.94); relative length of toes (order IV > V > III > II > I); tibiotarsal articulation of adpressed limb reaching the tip of snout; heels overlap when the tibias are perpendicular to the body axis, but not obvious; web on toes entire web; inner metatarsal tubercles oval and present, outer metatarsal tubercle absent, supernumerary tubercles absent, subarticular tubercles of toes oval and prominent, tips of toes expanded into discs slightly smaller than finger discs.

Dorsal surface of head smooth, lateral skin granular, with granules prominent and largest near the abdomen, ventral skin smooth; dorsolateral fold absent; pectoral gland absent; maxillary gland long and significant.

Colour of holotype in life. Dorsal surface mottled grass-green extending from the snout to the anterior part of the dorsum with mottled dark brown blotches covering the posterior part; flanks and lateral side of the head yellow with dark brown blotches (may vary across individuals to light yellow), flanks speckled with brownish-black spots; dorsal surface of limbs yellowish-brown with distinct dark brown alternating crossbands with crossbands on fore-limbs less prominent than those on hind-limbs; venter yellowish-white with light brown mottling concentrated on the throat and slightly present on the chest, belly and hind-limbs; iris with intricate golden reticulations forming a circumpupillary ring around the periphery (Fig. 3).

Colour of holotype in preservative. The mottled grass-green dorsum faded to whitish-grey while the mottled dark brown flanks and limbs slightly faded to whitish-brown with the brownish-black limb crossbars still clearly visible; the yellow colour on the flanks faded to olive-white with faded brownish mottles; the brownish-black crossbars on limbs are well-defined, but less vibrant than in life (Fig. 4).

Morphological variation. Measurements and morphological features of the paratype are provided in Table 4. The dorsal head surface, ventrum and limb surface smooth in paratype; the yellowish-white ventrum differs from having light brown mottles concentrated on the throat and slightly present on the chest, belly and hind-limbs in the holotype to ventrum yellowish-white with the throat, chest, belly and hind-limbs unmarked in the paratype.

Natural history. The new species was collected on rocks under shrubs along riverbeds and mountain streams at an altitude of approximately 1600 m a.s.l. No eggs or gravid females were found. Co-occurring within the same habitat were *Odorrana yunnanensis*, *Leptobrachella yingjiangensis* (Yang, Zeng & Wang, 2018), *Megophrys* sp., *Jingophrys feii* (Yang, Wang & Wang, 2018) and *Amolops afghanus* (Günther, 1858) (Fig. 8A).

Table 4. Measurements (in mm) of *Odorrana sudianensis* sp. nov. and *Odorrana heatwolei*. Abbreviations are defined in the Materials and Methods section.

Species	*Odorrana sudianensis* sp. nov. Holotype	*Odorrana sudianensis* sp. nov. Paratype	*Odorrana heatwolei*
Voucher Number	KIZ 058904	KIZ 058839	ITBCZ 3660
Sex	♀	♀	♂
SVL	85.3	78.9	50.8
HL	31.7	29.7	17.9
HW	29.4	26.8	16.9
HL/HW	1.08	1.11	1.06
SL	13.5	12.3	8.2
ED	9.5	9.4	7.2
SL/ED	1.42	1.31	1.14
IOD	6.6	6.5	4.6
UEW	8.0	7.1	5.7
IND	9.1	8.7	4.9
IOD/IND	0.73	0.75	0.94
NED	7.1	6.5	5.0
SND	5.4	4.9	3.3
SND/NED	0.76	0.75	0.66
UEW/IOD	1.21	1.09	1.23
TD	4.8	4.7	4.8
TD/ED	0.51	0.50	0.66
TYE	3.4	3.1	1.1
FAHL	42.5	38.8	26.5
HND	26.3	24	16.5
LAD	7.7	7.6	4.2
FAL	15.2	14.6	9.8
FIL	12.8	12.3	7.8
FIIL	11.6	10.9	6.8
FIIIL	17.7	16.7	11.8
FIVL	12.6	11.1	8.7
Relative length of fingers	3 > 1 > 4 > 2	3 > 1 > 4 > 2	3 > 4 > 1 > 2
HLL	152	145.1	44.7
FEM	45.6	41.8	28.9
TIB	48.7	46.9	31.6
FTL	46	43.9	26.5
TIL	10.1	10.0	7.8
TIIL	16.1	15.5	11.1
TIIIL	24.7	23.7	15.9
TIVL	33.1	33.1	23.0
TVL	27.6	26.7	16.7
Relative length of toes	4 > 5 > 3 > 2 > 1	4 > 5 > 3 > 2 > 1	4 > 5 > 3 > 2 > 1

Table 5. References for morphological characters for congeners of the genus *Odorrana* used in this study.

No.	Species name	Source
1	*Odorrana yunnanensis*	Rao (2022 "2020")
2	*Odorrana arunachalensis*	Saikia et al. (2017)
3	*Odorrana bolavensis*	Stuart and Bain (2005)
4	*Odorrana cangyuanensis*	Yang (2008)
5	*Odorrana dulongensis*	Liu et al. (2021)
6	*Odorrana gigatympana*	Orlov et al. (2006); Nguyen et al. (2018)
7	*Odorrana grahami*	Boulenger (1917)
8	*Odorrana indeprensa*	Bain and Stuart (2006)
9	*Odorrana jingdongensis*	Fei et al. (2001)
10	*Odorrana junlianensis*	Fei et al. (2009)
11	*Odorrana kuangwuensis*	Hu et al. (1966)
12	*Odorrana macrotympana*	Yang (2008); Liu et al. (2022)
13	*Odorrana margaretae*	Liu (1950)
14	*Odorrana monjerai*	Matsui and Jaafar (2006)
15	*Odorrana mutschmanni*	Pham et al. (2016)
16	*Odorrana orba*	Stuart and Bain (2005)
17	*Odorrana sinica*	Bain et al. (2003)
18	*Odorrana wuchuanensis*	Wu et al. (1983)

Distribution. The new species is currently known only from the type locality in Sudian, Yingjiang County, Yunnan Province, China (Fig. 1).

Comparisons. We compared *Odorrana sudianensis* sp. nov. with some of its nearest congeners and closely-related taxa as recovered from the phylogenetic data analyses while considering closely-related taxa and those whose mitochondrial DNA sequence data were currently unavailable. Additionally, since we only had two female specimens, we limited our morphological comparison to female characters documented for all the taxa included in the morphological analysis. In this case, we carefully examined morphological characters and conducted morphological comparisons of the new species with its sister species *O. dulongensis* as well as all the species recovered within the larger clade (clade E), consisting of *O. margaretae*, *O. kuangwuensis*, *O. jingdongensis*, *O. yunnanensis*, *O. grahami*, *O. junlianensis*, *O. mutschmanni* and *O. wuchuanensis*. Moreover, we conducted morphological comparisons with species lacking sequence information, such as *O. arunachalensis*, *O. bolavensis*, *O. cangyuanensis*, *O. gigatympana*, *O. indeprensa*, *O. orba*, *O. sinica* and *O. monjerai* described solely based on morphology and species also known to occur in Yingjiang County, Yunnan Province, China, such as *O. yunnanensis* and *O. macrotympana* (Yang, 2008).

Odorrana sudianensis sp. nov. differs from *O. dulongensis* by flanks yellow with dark brown blotches (vs. flanks light yellow with black spots); ventrum with light brown mottles on throat and faintly on belly and hindlimbs, but not obvious (vs. ventrum unmarked except for light throat mottling); distinct black spots on upper jaw absent (vs. present); supratympanic fold obvious, weak and short (vs. supratympanic fold distinct); supernumerary tubercles present and rounded (vs. indistinct); finger lengths III > I > IV > II (vs. finger lengths III > IV > II = I, Fig. 5).

Odorrana sudianensis sp. nov. is similar in appearance to *O. yunnanensis*; however, it differs by having a smaller body size SVL 78.9–85.3 mm (vs. 82.3–107.2 mm in adult females); finger discs significantly expanded (vs. finger discs small); absence of a small white dot between the anterior corners of the two eyes (vs. present); and relative length of fingers III > I > IV > II (vs. relative length of fingers III > IV > I = II); from *O. margaretae* by smaller body size SVL 78.9–85.3 mm (vs. a large body size SVL 93.0–113.0 mm in females); dorsum granular to smooth in some individuals, anteriorly mottled grass-green with mottled dark brown blotches on the posterior region (vs. dorsum smooth, dark green with no spots); fingers III > I > IV > II (vs. relative length of fingers III > IV > I > II); from *O. kuangwuensis* by lack of spots on the toe and finger webbing (vs. present); larger body size SVL 78.9–85.3 mm (vs. smaller SVL 66.0–71.4 mm in females); from *O. jingdongensis* by a smaller body size SVL 78.9–85.3 mm (vs. a larger body size SVL

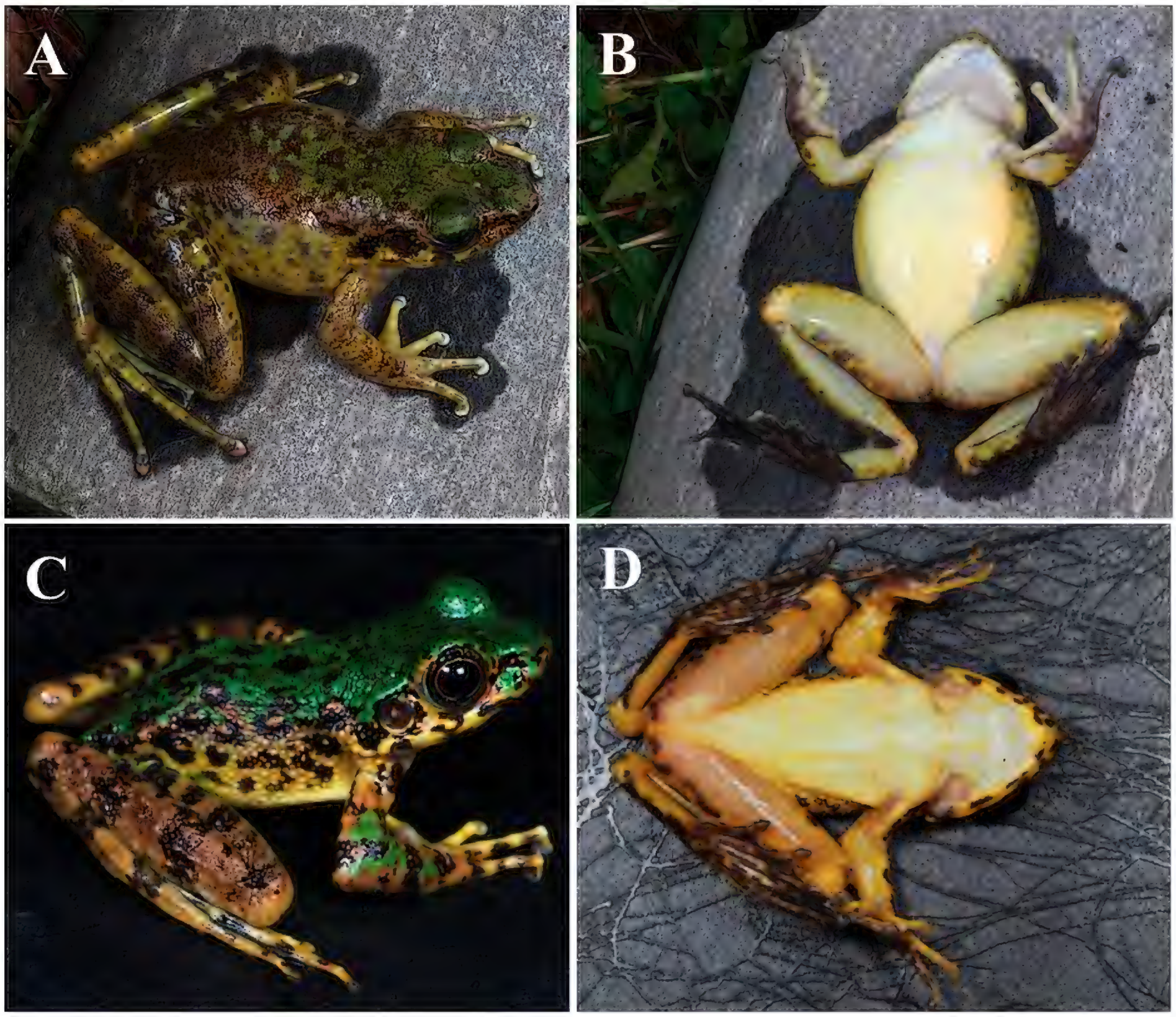

Figure 5. Comparison of morphological characteristics with congeners. **A.** Dorsal and **B.** Ventral views of *Odorrana sudianensis* sp. nov. paratype KIZ058839 (female) in life; **C.** Dorsal and **D.** Ventral views of *Odorrana dulongensis* holotype (male) in life; photos by Shen-Pin Yang and Xiao-Long Liu.

98.0 mm in females); dorsal surface of head smooth, lateral skin granular, with granules prominent and largest near the abdomen (vs. dorsum covered with moles and scattered large warts from the snout to the vent); relative length of fingers III > I > IV > II (vs. relative length of fingers III > IV > I > II); from *O. grahami* by having the tip of fingers expanded into discs, with disc largest in the third finger, circum-marginal grooves, all finger discs expanded with lateroventral grooves (vs. fingertips and toe tips not expanded and lateroventral grooves absent); smaller adult body size SVL 78.9–85.3 mm (vs. larger body size with SVL 89–107 mm in females); a small white spot between the anterior corners of the two eyes (vs. absent); relative length of fingers III > I > IV > II (vs. relative length of fingers III > IV > I = II); from *O. junlianensis* by a smaller adult body size SVL 78.9–85.3 mm (vs. a large body size SVL 87.2–102.0 mm in females); relative length of fingers III > I > IV > II (vs. relative length of fingers III > IV > I = II); from *O. mutschmanni* by smaller body size with SVL 78.9–85.3 mm (vs. a large body size SVL 108.7–110.1 mm in females); from *O. wuchuanensis* by tympanum well defined, smaller and half the eye diameter (vs. tympanic membrane large and 4/5 of the eye diameter); dorsum anteriorly mottled grass-green with mottled dark brown blotches on the posterior region (vs. dorsum green with scattered dark spots some with pale golden edges); ventral surface yellowish-white with light brown mottles concentrated on the throat and slightly present on the chest belly and hind-limbs, but not obvious across individuals (vs. ventral mask dark grey and light golden yellow with large patches intertwined into a network); from *O. arunachalensis* by the absence of a black inter-orbital band (vs. presence of a black inter-orbital band); absence of a pair of discontinuous, black dorso-lateral bands (vs. present); head length longer than head width (vs. head broader than long); tympanum well defined, smaller, half the eye diameter (vs. tympanum small and depressed, 1/3 of the eye); dorsum anteriorly mottled grass-green with mottled dark brown blotches on the posterior region with skin granular to smooth in some individuals (vs. dorsum completely green with brown mottling in female, smooth, with few weak granules on the flanks); relative lengths of fingers III > I> IV > II (vs. relative finger lengths: III > IV > II > I); from

O. bolavensis by dorsal skin granular to smooth in some individuals (vs. dorsal skin shagreened with spinules); relative lengths of fingers III > I > IV > II (vs. relative lengths of fingers III > IV > I > II); from *O. cangyuanensis* by dorsum anteriorly mottled grass-green with mottled dark brown blotches on the posterior region (vs. dorsum uniform brown or brownish-black); relative lengths of fingers III > I > IV > II (vs. III > II > IV > I); from *O. gigatympana* by having a larger adult female body size SVL 78.9–85.3 mm (vs. a smaller body size SVL 58.0–67.7 mm in females); dorsum anteriorly mottled grass-green (vs. dorsum uniform brown or grey); flanks and lateral side of the head yellow with dark brown blotches (vs. flanks brown with dark spots); absence of a black stripe extending from the tip of the snout to the eye and from behind the eye above the tympanum to axilla (vs. present); relative lengths of fingers III > I > IV > II (vs. III > IV > II > I); dorsolateral folds absent (vs. presence of distinct dorsolateral folds); absence of the outer metatarsal tubercle (vs. present); from *O. indeprensa* by a smaller body size SVL 78.9–85.3 mm (vs. a larger body size SVL 92.8–101 mm); from *O. orba* by dorsal surface and lateral flanks of skin granular (vs. dorsal skin heavily shagreened with some large tubercles); absence of dorsolateral folds (vs. presence of weakly visible dorsolateral folds in females); relative lengths of fingers III > I > IV > II (vs. relative finger lengths III > IV > I > II); from *O. sinica* by dorsal and lateral flanks of skin granular to smooth in some individuals (vs. smooth); tympanum distinct and well defined (vs. tympanum indistinct and skin-covered); larger body size SVL 78.9–85.3 mm (vs. smaller body size, SVL of single mature female is 66.6 mm); from *O. monjerai* by the anterior part of dorsum mottled grass-green with mottled dark brown blotches on the posterior region (vs. dorsum uniform brown or grey and unspotted); absence of dorsolateral folds (vs. presence of distinct dorsolateral folds); dorsal and lateral flanks of skin granular skin (vs. finely tuberculated dorsal skin); from *O. macrotympana* by having the anterior part of the dorsum mottled grass-green with mottled dark brown blotches on the dorsal and lateral flanks (vs. dorsum greyish-brown, brownish-green or solid green with a few or many tiny black spots); dorsal and lateral flanks of skin granular to smooth in some individuals (vs. smooth dorsal skin); absence of dorsolateral folds (vs. presence of distinct dorsolateral folds); relative lengths of fingers III > I > IV > II (vs. relative finger lengths III > IV > I > II).

Odorrana heatwolei (Stuart & Bain, 2005)

Figs 6, 7

Chresonymy. *Rana heatwolei* Stuart & Bain, 2005.

Rana tiannanensis — Ohler 2007 (part).

Odorrana heatwolei — Poyarkov et al. 2021; Liu et al. 2023; Stuart, Seateun, Sivongxay & Phimmachak, 2024.

Common name. Heatwole's Odorous Frog (Stuart et al. 2024)

Type specimens of *O. heatwolei*. *Holotype*: Adult male, Voucher number FMNH 258134, based on the original description (Stuart and Bain 2005) and an updated diagnosis (Liu et al. 2023).

Specimen examined. Adult male ITBCZ 3660, collected from Loi 1 Village, Muong Loi Commune, Dien Bien Province, Vietnam by Luan Thanh Nguyen and Hung Van Lo on 6 January 2019 (20°56.2431'N, 103°14.55882'E; 700 m a.s.l).

Morphological diagnosis. Species measurements are provided in Table 4. ITBCZ 3660, adult male; body relatively robust (SVL 50.8 mm); head length slightly longer than wide (HL/HW 1.06); dorsum shagreened with skin smooth on limbs and venter, skin on flanks heavily granular; snout pointed in dorsal view and rounded in profile, projecting beyond the lower jaw; canthus rostralis distinctly visible; loreal region concave; nostrils lateral, closer to the tip of the snout than to eye (SND/NED 0.66); pineal body distinct; eye large and prominent (ED 7.2 mm) with a golden iris; upper eyelid width greater than interorbital distance (UEW/IOD 1.23); internasal distance greater than interorbital distance (IOD/IND 0.94); snout length greater than the eye diameter (SL/ED 1.14); tympanum large, round and distinct (TD/ED 0.66), tympanic rim round and distinct, supratympanic fold curving slightly above and behind the tympanum; dorsolateral folds distinct extending close to vent; vomerine teeth distinct in two oblique ridges between choanae; tongue cordiform, deeply notched posteriorly with the anterior portion attached to the floor of the mouth; vocal sac opening at corner of mouth, external vocal sacs present.

Fore-limbs robust; fingers long and slender; no webbing on fingers; tips of all four fingers expanded into discs with circum-marginal grooves, relative length of fingers III > IV > I > II; inner and outer metarcarpal tubercles present; nuptial pad on the base of the first finger present; subarticular tubercles well developed, supernumerary tubercles at the base of fingers II, III and IV. Hind-limbs long and moderately muscular; toes long and slender; tips of toes slightly expanded into discs; toes fully webbed to the base of disc; relative toe lengths IV > V > III > II > I; subarticular tubercles oval and prominent; inner metatarsal tubercle oval and prominent, outer metatarsal tubercle absent; heels perpendicular to the body axis when hind-limbs are adpressed. Dorsal skin surface shagreened, flanks granular; ventral skin smooth.

Colouration in life. Dorsum brown with distinct, small, darker brown spots; upper and lower lip creamy-white; limbs brown with distinct dark crossbars; iris golden; ventral skin creamy-white, with fine brown mottling concentrated along the throat, chest and lateral margins.

Colouration in preservative. The dorsum darkened with the small darker brown spots turning black, but still visible across the dorsal surface; dorsal surfaces of limbs darkened to black, with the original limb crossbars becoming indistinct; the ventral surfaces of the head, fore-limbs, chest, belly and hind-limbs faded to a fleshy creamy-white colour.

Comparative remarks. Observed morphological characters for this specimen align closely with the male

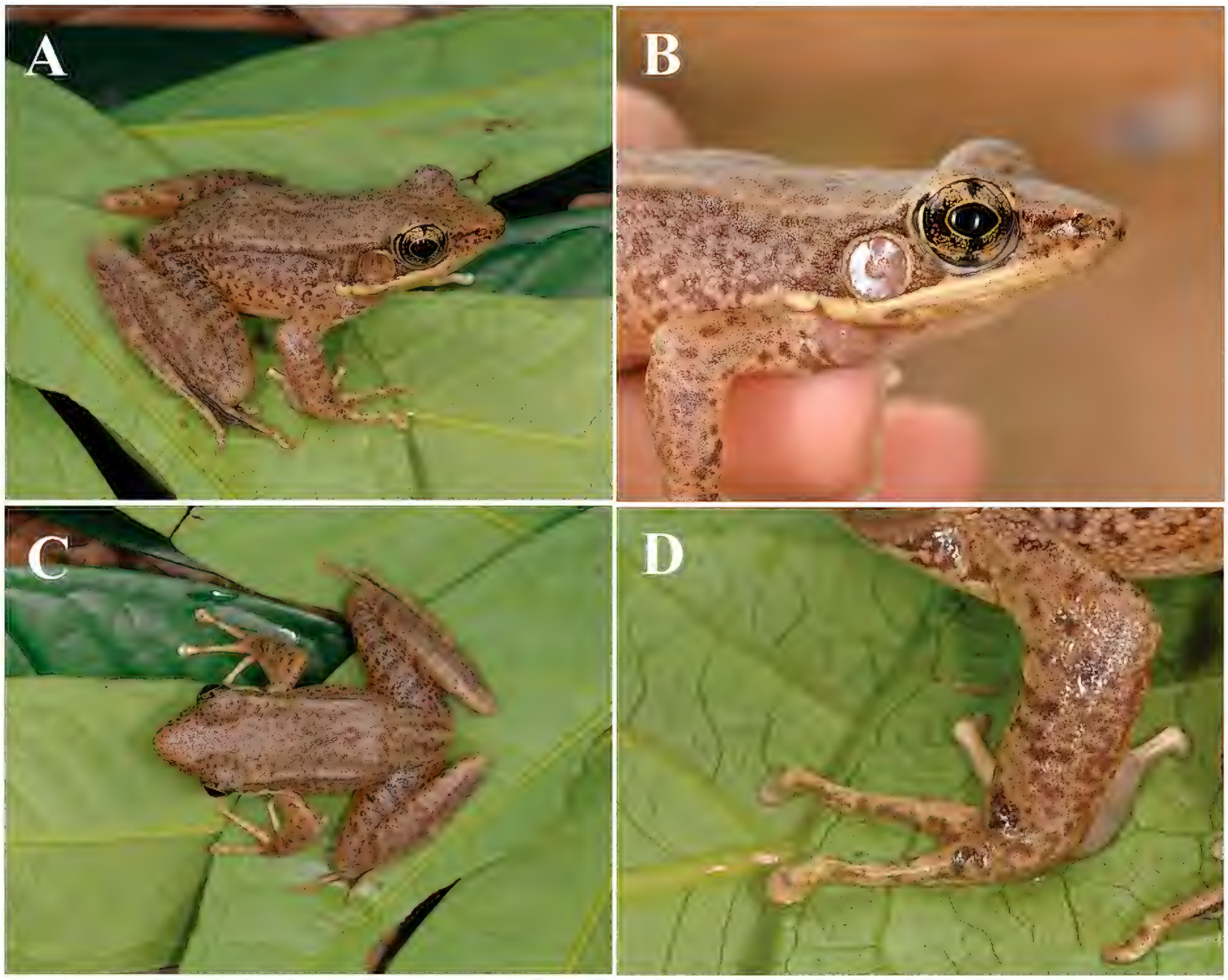

Figure 6. Adult male *Odorrana heatwolei* (ITBCZ 3660) from Muong Loi Commune, Dien Bien Province, Vietnam in life. **A.** Dorsolateral view; **B.** Lateral view of the head region; **C.** Dorsal view; **D.** Dorsal view of fore-limb; photos by Luan Thanh Nguyen.

holotype description of *O. heatwolei* from Phongsaly, Laos and male specimens from Yunnan, China, in all the key adult diagnostic traits (Stuart and Bain 2005; Liu et al. 2023). The measured morphological characters (e.g. SVL, HL, HW, TD, ED, dorsal skin texture, tympanum visibility and presence of dorsolateral folds in males) of the male specimen described herein are within the variation reported for the Lao's type series (Stuart and Bain 2005; Liu et al. 2023), including the finger and toe lengths and overall morphology. However, the slight differences in body size variation and dorsal colouration, including less contrasting blotches, may reflect age, regional or habitat-related variation rather than taxonomic distinction.

Natural history. This species inhabits forest streams and river banks between 600 m and 1200 m a.s.l. It was reported in secondary growth disturbed forest, in approximately 8 m wide rocky forest streams in north-western Vietnam (Dien Bien Province) near the Laos border (Stuart and Bain 2005) (Figs 1, 8B). Additionally, it was collected in nature trails at 1161 m a.s.l. in Phu Hin Rong Kla National Park, Phitsanulok Province, Thailand. The low-gradient rocky streams bordered by dense broadleaf forest and shrub cover with slow to moderately flowing water and vegetation along the banks seem to be an ideal habitat offering both terrestrial and aquatic microhabitats for this species. Specimens collected during nocturnal surveys were found either on low vegetation or rocks near flowing water, suggesting a strong association with riparian zones.

Distribution. The species was only known from its type locality in Phou Dendin National Biodiversity Conservation Area, Phongsaly Province, Laos and the Xishuangbanna Prefecture, Yunnan Province, China. This study constitutes the first confirmed records of *O. heatwolei* in Vietnam and northern Thailand, extending the species' known range eastwards to Vietnam and south-westwards into Thailand from the type locality in northern Laos (Fig. 1).

Remarks. *Odorrana heatwolei* was originally described from the Nam Ou River in the Phou Dendin National Biodiversity Conservation Area, Phongsaly District, Phongsaly Province, Laos (22°5.63333'N, 102°12.83333'E) at an elevation of 600 m. Its known distribution includes Laos and parts of China, where it is a natural resident. However, Ohler (2007) placed

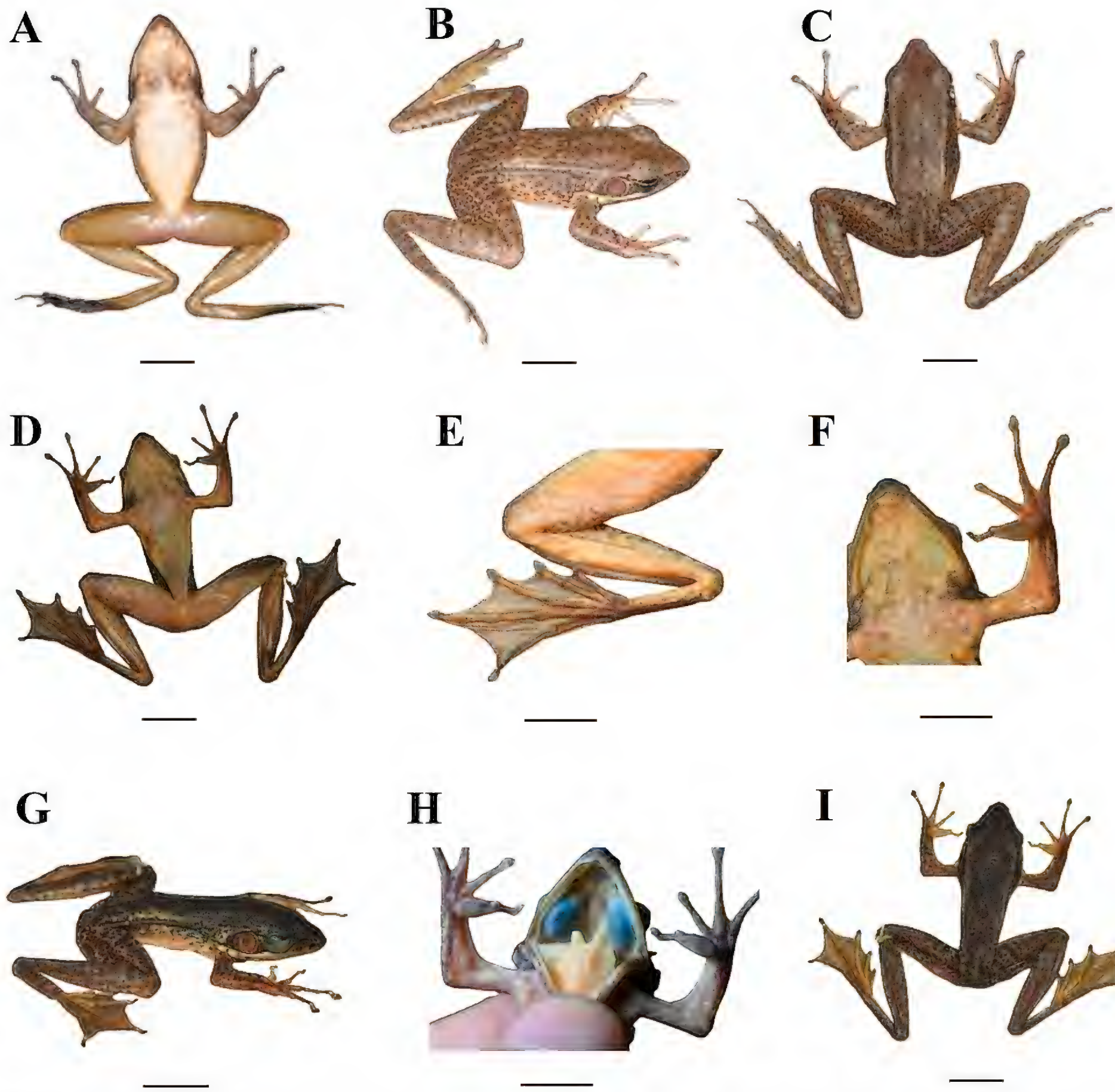

Figure 7. Photos of *Odorrana heatwolei* specimen (ITBCZ 3660) before preservation. **A.** Ventral view; **B.** Dorsolateral view; **C.** Dorsal view; after preservation; **D.** Ventral view; **E.** Ventral view of hind-limb; **F.** Ventral view of head and fore-limb; **G.** Lateral view; **H.** Ventral view of fore-limbs and the oral cavity; **I.** Dorsal view. Photos by Luan Thanh Nguyen. Scale bars: 10 mm.

O. heatwolei under the synonymy of *O. tiannanensis*. This synonymisation was later challenged by Liu et al. (2023), who re-instated *O. heatwolei* as a distinct species based on molecular data, identifying it as the sister taxon to *O. tiannanensis*. Additionally, Poyarkov et al. (2021) expressed doubt about the proposed synonymy, recommending further evidence to clarify the taxonomic status of the species. Our molecular analyses, based on 16S sequence data, recovered samples collected from Thailand and Vietnam as *O. heatwolei* after strongly clustering with the topotypic sequences of *O. heatwolei* (BPP = 1; BS = 100). This finding establishes the first record of *O. heatwolei* in both Thailand and Vietnam, specifically from northern Thailand (Tambol Don Paya, Ban Sapan, Amphoe Bo Kluea), near the Laos border, Phitsanulok Province, Thailand and Dien Bien Province in Vietnam, extending its currently known distribution further from Laos and China. Genetic distance analyses further supported its distinction from *O. tiannanensis* and confirmed its taxonomic identity as *O. heatwolei* as discussed in detail in the results section.

Odorrana bacboensis (Bain, Lathrop, Murphy, Orlov & Ho, 2003)

Chresonymy. *Rana* (*Odorrana*) *bacboensis* Bain et al. 2003.

Huia bacboensis — Frost et al. 2006.

Odorrana bacboensis — Chen et al. 2005; Che et al. 2007; Stuart 2008; Wang et al. 2015.

Common name. Tonkin Odorous Frog (Poyarkov et al. 2021).

Figure 8. A. Habitat of *Odorrana sudianensis* sp. nov. from the type locality in Yingjiang, Yunnan, China; photo by Zhong-Bin Yu; **B.** Habitat of *Odorrana heatwolei* in Muong Loi Commune, Dien Bien, Vietnam; photo by Luan Thanh Nguyen.

Remarks. The taxonomic placement and distribution of *O. bacboensis* from China has been disputed, with Poyarkov et al. (2021) recommending verification for the presence of this species in China. The type locality for *O. bacboensis*, based on the original description, is the Khe Moi River, Con Cuong Village, Con Cuong District, Nghe An Province, Vietnam. However, Wang et al. (2015) reported it as a new country record for China with samples collected from Hekou County, Yunnan, and Bainan Village, Napo County, Guangxi, indicating a range extension from northern-central Vietnam to south-eastern Yunnan and the adjacent area in Guangxi Province, China. Molecular analyses recovered these *Odorrana* samples by Wang et al. (2015) within the true *O. bacboensis* subclade (BPP = 1; BS = 100) (see clade B) clustering with the paratype sequence (GenBank accession number DQ650569; voucher FMNH 255611) collected from the type locality Khe Moi, Nghe An, Vietnam, thus supporting the presence of the species in both mainland China and Vietnam.

***Odorrana fengkaiensis* Wang, Lau, Yang, Chen, Liu, Pang, & Liu, 2015**

Chresonymy. *Odorrana fengkaiensis* Wang et al. 2015.

Odorrana fengkaiensis — Pham et al. 2020.

Common name. Fengkai Cascade Frog (Pham et al. 2020)

Remarks. Wang et al. (2015) described a distinct lineage, *O. fengkaiensis*, while citing similarity and a moderate level of mitochondrial sequence divergence (1.9–2.4%) from *O. hainanensis* Fei, Ye & Li, 2001. Although low to moderate genetic distances have been observed to indicate clear species boundaries in some species within *Odorrana* (e.g. *O. jingdongensis* and *O. yunnanensis*) the validity of *O. fengkaiensis* in respect to some records reported from Vietnam has been questioned (Poyarkov et al. 2021).

Wang et al. (2015) described *O. fengkaiensis*, based on the holotype specimen recorded from Heishiding Nature Reserve, Fengkai County, Guangdong Province, China. Pham et al. (2020) reported *O. fengkaiensis* from north-eastern Vietnam; however, this record was disputed as a likely misidentification with specimens of *O. hainanensis* by Poyarkov et al. (2021). We utilised sequences directly submitted to GenBank from northern Vietnam as *O. bacboensis* (GenBank accession numbers KX893887, voucher IEBR A.2015.83; KX893888, voucher VFUKH 073 and KX893909; voucher IEBR 3942). These sequences were recovered within the true *O. fengkaiensis* subclade containing the paratype sequences with strong node support values (BPP = 1; BS = 100) (see clade B). *Odorrana hainanensis* was recovered as a closely-related, but distinct lineage from *O. fengkaiensis* (BPP = 1; BS = 99). However, to fully resolve the evolutionary relationship within these taxa, comprehensive geographic sampling across Vietnam and China, a careful re-examination of the voucher specimens and the use of genome-wide sequence data should be considered in the future.

***Odorrana hejiangensis* (Deng & Yu, 1992)**

Chresonymy. *Rana hejiangensis* Deng & Yu, 1992.

Huia hejiangensis — Fei & Ye, 2001; Frost et al. 2006.

Odorrana hejiangensis — Che et al. 2007.

Odorrana (*Odorrana*) *nanjiangensis* Fei, Ye, Xie & Jiang, 2007.

Odorrana nanjiangensis — Zhu 2016; Zhang et al. 2021; Dufresnes and Litvinchuk 2022.

Common name. Hejiang Odorous Frog (Fei 1999).

Remarks. *Odorrana hejiangensis* was originally described from Shunyangxi, Hejiang County, Sichuan Province, China, with its known distribution extending across northern Guizhou and western Guangxi Provinces, China (Frost 2025). Our analyses placed the topotypic sequences of *O. hejiangensis* and *O. nanjiangensis* within the same strongly supported subclade (BPP = 1; BS = 100) (see clade B). The topotype sequence of *O. nanjiangensis* (accession number KF185042.1; voucher HNNU1007-291) was collected from Nanjiang, Sichuan Province, China, whereas the *O. hejiangensis*

topotype sequence (accession number KF185052; voucher HNNU1007-202) was collected from Hejiang, Sichuan Province, China, as deposited by Chen et al. (2013). Previous studies, including Dufresnes and Litvinchuk (2022), reported nearly identical mitochondrial sequences between these two species, with a genetic distance of only 0.1%. While the possibility of misidentification for the sole available 16S representative sequence of *O. nanjiangensis* cannot be entirely ruled out, we hypothesise that these taxa are conspecific. Consequently, we propose synonymising *O. nanjiangensis* with the senior synonym *O. hejiangensis*, which holds taxonomic priority. However, to definitively resolve this issue, a thorough examination of respective voucher specimens is necessary to identify any diagnostic characters between the two species.

***Odorrana jingdongensis* Fei, Ye, & Li, 2001**

Chresonymy. *Odorrana jingdongensis* Fei, Ye & Li, 2001.
Rana (*Odorrana*) *hmongorum* Bain et al. 2003.
Huia jingdongensis — Frost et al. 2006.
Huia hmongorum — Frost et al. 2006.
Odorrana hmongorum — Chen et al. 2005; Che et al. 2007; Stuart 2008.
Odorrana jingdongensis Chen et al., 2005; Che et al. 2007; Poyarkov et al. 2021; Stuart, Seateun, Sivongxay & Phimmachak, 2024.

Common name. Jingdong Odorous Frog (Stuart et al. 2024).

Remarks. This species is known by original designation from its type locality in Xinminxiang, Jingdong County, Yunnan Province, China. However, its current distribution is recognised to extend to Dien Bien, Ha Giang, Lai Chau, Son La and Lao Cai Provinces in northern Vietnam owing to the synonymisation of *O. hmongorum* originally described from Sa Pa Village, near O Qui Ho Pass, Lao Cai Province, Vietnam by Ohler (2007). Moreover, this proposed synonymy with *O. jingdongensis* requires further evidence (Poyarkov et al. 2021; Stuart et al. 2024). Based on our phylogenetic analyses, the subclade comprising *O. jingdongensis*, *O. junlianensis*, *O. yunnanensis*, *O. kuangwuensis*, *O. margaritae*, *O. hmongorum* and *O. grahami* is weakly supported (BPP < 0.98; BS = 88) (see clade E). This result does not support the synonymy of *O. jingdongensis* and *O. hmongorum*; thus, a detailed study is needed to properly delimit species boundaries within it. Moreover, Yuan et al. (2023) demonstrated instances of rampant mitochondrial genome introgression and reported an unidentified lineage believed to be *O. hmongorum* within the *O. grahami* complex. The study revealed cases of mitonuclear discordance that mask the distinctiveness of closely-related taxa, therefore highlighting the need for integrative taxonomic approaches to properly clarify the taxonomic position of species within this challenging group.

Discussion

Species discovery within *Odorrana* has been on the increase with new species and new country records reported yearly. Despite significant progress, our discovery of *Odorrana sudianensis* sp. nov. that aligns with several studies that diversity within the genus remains significantly underestimated (Pham et al. 2016; Liu et al. 2021; Li et al. 2024). This addition brings the total number of species under the genus to 67 and those known from China to 46.

Six *Odorrana* species are currently recognised in Thailand (Frost 2025), including *O. yunnanensis*, *O. livida* (Blyth, 1856), *O. chloronota* (Günther, 1876), *O. hosii* (Boulenger, 1891), *O. aureola* Stuart, Chuaynkern, Chanard & Inger, 2006 and the endemic *O. indeprensa*. Comparatively, 22 species of the genus *Odorrana* have been documented in Vietnam, including two endemic species, *O. gigatympana* and *O. mutschmanni*. Our results revealed that *O. heatwolei* also occurs in Thailand and Vietnam, raising the total number of *Odorrana* species known from both countries to seven and 23, respectively. Notably, amphibian discoveries in Thailand have been increasing, with several studies documenting range extension for various amphibian taxa (Poyarkov et al. 2021; Cao et al. 2024; Pomchote et al. 2024). The discovery of *O. heatwolei*, earlier known from Phou Dendin National Biodiversity Conservation area, Phongsaly Province in Laos and the nearby Xishuangbanna Prefecture, Yunnan Province, China, extends its geographic range to northern Thailand in Nan and Phitsanulok Provinces and Dien Bien Province in north-western Vietnam. These findings suggest that *O. heatwolei* is likely more widespread across the Indochinese Region than previously reported. It also highlights the importance of scientific collaborations, field surveys and the use of molecular taxonomy to properly delimit and understand amphibian diversity across Indochina. Further surveys within the northern and north-eastern border areas of Thailand and northern and central Laos and Vietnam are necessary to uncover additional populations and accelerate amphibian discovery.

Moreover, our study clarified the taxonomic placement of several species within *Odorrana* and proposed synonymising *O. hejiangensis* with *O. nanjiangensis*, confirmed the presence of *O. bacboensis* in China, proposed revisiting the synonymy of *O. jingdongensis* and *O. hmongorum* and clarified the taxonomic distinction between *O. tiannanensis* and further *O. heatwolei* as herein discussed.

Conclusions

Indochina plays a key role as a global biodiversity hotspot with many amphibian species documented within its borders. Although significant progress has been made in studying amphibian diversity across Indochina, intensifying research efforts through scientific collaborations, extensive field surveys and addressing gaps in poorly-studied taxa could enhance species discovery

and strengthen conservation measures for the region's amphibians. Furthermore, a more integrative approach coupled with extensive sampling, genome-wide sequence data, morphology and bioacoustics is necessary in the future to accurately delimit species boundaries and clarify taxonomic uncertainties not only within *Odorrana*, but also other amphibian genera.

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Supplementary material 1

Genetic distance

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Data type: xlsx

Explanation note: Between-group mean genetic distances based on 16S gene fragment for all Odorrana species used in this study. Standard error estimates are shown above the diagonal.

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Link: https://doi.org/10.3897/zse.101.162366.suppl1

Supplementary material 2

Phylogenetic trees

Authors: Felista Kasyoka Kilunda, Shen-Pin Yang, Luan Thanh Nguyen, Manh Van Le, Chatmongkon Suwannapoom, Bryan L. Stuart, Sang Ngoc Nguyen, An-Ru Zuo, Ding-Can Zhang, Zheng-Pan Duan, Pei-Wen Duan, Zhong-Bin Yu, Yun-He Wu, Jing Che

Data type: pdf

Explanation note: Maximum Likelihood (ML) and Bayesian Inference (BI) phylogenetictrees of the genus Odorrana inferred by 16S rRNA mitochondrial-gene fragment.

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Link: https://doi.org/10.3897/zse.101.162366.suppl2